Comparative osteological study of three species of distinct genera of Haplotilapiini (Cichlidae)

by

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Abstract. – In palaeontological and archaeozoological studies dealing with tilapia remains, identifications are usually limited to the level of the tribe Tilapiini (now called Haplotilapiini). In the present study, dry skeletons of *Oreochromis niloticus* (Linnaeus, 1758), *Oreochromis aureus* (Steindachner, 1864), *Sarotherodon galilaeus* (Linnaeus, 1758) and *Coptodon zillii* (Gervais, 1848) were analysed with the aim of defining morphological characters on a series of isolated skeletal elements. Eighteen different skeletal elements that have good chances of being well preserved (and of being recognised as tilapia) were analysed, *i.e.* premaxilla, dentary, maxilla, articular, lacrimal, palatine, quadrate, hyomandibula, operculum, preoperculum, posttemporal, cleithrum, supracleithrum, urohyal, vomer, and the first three precaudal vertebrae. Diagnostic criteria are described and illustrated with figures. It appears from the comparative analysis, and also from blind tests carried out afterwards, that identification is possible except for the articular and the third vertebra. More accurate identification of fossil and subfossil finds of Haplotilapiini should allow a better documentation of the zoogeographical history of these taxa in the future.

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Received: 15 Dec. 2016
Accepted: 8 Jun. 2017
Editor: O. Otero

Résumé. - Ostéologie comparée de trois espèces de genres différents de Haplotilapiini.

Dans les études paléontologiques et archéozoologiques, l'identification des restes de tilapias se limite le plus souvent au niveau de la tribu Tilapiini (ou maintenant Haplotilapiini). Dans la présente étude, nous examinons des squelettes d'*Oreochromis niloticus* (Linnaeus, 1758), *Oreochromis aureus* (Steindachner, 1864), *Sarotherodon galilaeus* (Linnaeus, 1758) et *Coptodon zillii* (Gervais, 1848) dans le but de définir des caractères morphologiques distinctifs sur une série d'éléments squelettiques isolés. Dix-huit éléments généralement bien conservés dans les contextes archéologiques et paléontologiques, et qui sont reconnaissables comme appartenant à des tilapias, ont été analysés, notamment le prémaxillaire, le dentaire, le maxillaire, l'articulaire, le lacrymal, le palatin, le carré, l'hyomandibulaire, l'opercule, le préopercule, le post-temporal, le cleithrum, le supracleithrum, l'urohyal, le vomer et les trois premières vertèbres. Les critères diagnostiques sont décrits et illustrés par des figures. L'étude comparative ainsi que des tests en aveugle montrent qu'une identification est possible pour tous les éléments squelettiques considérés, sauf pour l'articulaire et la troisième vertèbre. Dès maintenant, des identifications plus précises des restes fossiles et archéozoologiques d'Haplotilapiini sont possibles ; elles devraient permettre de mieux documenter l'histoire zoogéographique de ces taxons.

Key words
Cichlidae
Haplotilapiini
Oreochromis
Sarotherodon
Coptodon
Osteology

Studies into the fossil record and biogeography of Cichlidae on a global (Murray, 2001) or an African (Stewart, 2001) scale explicitly mention the difficulties to identify taxa within this family as a result of the dearth of comparative osteological data. Cichlidae fossil finds compiled in the aforementioned review articles are most often not identified beyond family level, and if they are, then they are mainly labelled as Tilapiini or as *Tilapia* sp., the latter designation meaning Tilapiini as well. According to the latest phylogeny (Dunz and Schlieven, 2013) the species discussed here should be labelled as Haplotilapiini. When dealing with rather well preserved and articulated fossils of that tribe, the ichthyological literature (Trewavas, 1983) can be helpful to recognise the genera retained in that revision, namely *Oreochromis* Günther, 1889, *Sarotherodon* Rüppell, 1852 and *Tilapia* Smith, 1840 (below we use *Coptodon* Gervais, 1853). Trewavas (1983: 16-19) mentions (slight) differences in the number of vertebrae and in the vomer-supraethmoid that are connected in *Coptodon* and not in *Sarotherodon* and *Oreochromis*. She also mentions that the teeth of the jaws are coarser in *Coptodon* than in the two other genera.

A detailed description of the osteology of *Coptodon guineensis* (Günther, 1862) has been given by Vandewalle (1972), while Chardon and Vandewalle (1971) described the differences in cranial morphology of five tilapia species that can be related to spawning behaviour (substrate versus mouth breeding). However, the literature hardly mentions any osteological features that allow identification of single bone elements. Such criteria would be helpful to identify the more frequently encountered isolated fish bones from archaeological and Quaternary palaeontological sites. The only exception is in Murray and Stewart (1999), where criteria are mentioned for the supraoccipital, hyomandibula, cleithrum, supracleithrum, posttemporal and predorsal bone that

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Cybium 2017, 41(3): 223-235.

allow distinguishing the genera *Oreochromis*, *Sarotherodon* and *Coptodon*.

The aim of the present comparative study is to document additional diagnostic criteria allowing to differentiate isolated skeletal elements of these taxa, using series of dry, desarticulated skeletons of *Oreochromis niloticus* (Linnaeus, 1758), *Oreochromis aureus* (Steindachner, 1864), *Sarotherodon galilaeus* (Linnaeus, 1758) and *Coptodon zillii* (Gervais, 1848). As these taxa co-occur over a vast area, extending even beyond the Nilo-Sudan ichthyofaunal province, the diagnostic criteria will be useful to reconstruct the zoogeographical history of these fish in more detail.

MATERIAL AND METHODS

The collection of dry, disarticulated fish skeletons presently housed at the Royal Belgian Institute of Natural Sciences contains more than 700 Haplotilapiini specimens that were mainly collected by the last author from the Egyptian Nile, the Niger River near Niamey and the Senegal River. For the comparative study conducted here, the best represented species are used, namely *Oreochromis niloticus* (511 specimens ranging in size between 5.1 and 45 cm SL), *Sarotherodon galilaeus* (28 specimens between 5.0 and 28 cm SL) and *Coptodon zillii* (175 specimens between 5.3 and 18 cm SL). Of each species, between 11 and 14 individuals of different sizes were selected and in each case the largest specimens in the collection were included (Tab. I). In addition, after the comparative study, all three *O. aureus* specimens in the collection (ranging in size between 11.0 and 15.0 cm SL) were considered in order to verify if the criteria defined for *O. niloticus* hold when another species of the same genus is considered.

The 18 skeletal elements that were retained for study are those of which we know by experience that they have good chances of being well preserved (and being recognised as tilapia) in an archaeological or palaeontological context. These elements are the premaxilla, dentary, maxilla, articular, lacrimal, palatine, quadrate, hyomandibula, operculum, preoperculum, posttemporal, cleithrum, supracleithrum, urohyal, vomer, and the first three precau-

Table I. – Dry skeletons used for the comparative study, with indication of species, register number (of the Royal Museum of Central Africa, Tervuren; RMCA), standard length (SL), total length (TL), and locality.

Species	Register number	SL (cm)	TL (cm)	Locality
Coptodon zillii	RMCA 94-010-P-0052	8.5	11.0	Esna, Egypt
Coptodon zillii	RMCA 93-158-P-0045	9.5	12.0	Esna, Egypt
Coptodon zillii	RMCA 94-010-P-0038	9.5	12.0	Esna, Egypt
Coptodon zillii	RMCA 93-158-P-0044	10.5	13.0	Esna, Egypt
Coptodon zillii	RMCA 88-023-P-0409	12.0	14.5	Lake Fayum, Egypt
Coptodon zillii	RMCA 92-140-P-0004	12.0	15.0	Esna, Egypt
Coptodon zillii	RMCA 93-087-P-0055	12.0	15.0	Luxor, Egypt
Coptodon zillii	RMCA 92-140-P-0003	14.0	17.0	Esna, Egypt
Coptodon zillii	RMCA 92-140-P-0002	15.0	19.0	Esna, Egypt
Coptodon zillii	RMCA 92-140-P-0001	16.0	20.0	Esna, Egypt
Coptodon zillii	RMCA 90-039-P-0060	18.0	22.5	Ndiama, Senegal
Oreochromis aureus	RMCA 88-023-P-0427	11.0	14.0	Lake Edku, Egypt
Oreochromis aureus	RMCA 88-023-P-0425	14.5	18.5	Lake Edku, Egypt
Oreochromis aureus	RMCA 88-023-P-0426	15.0	19.0	Lake Edku, Egypt
Oreochromis niloticus	RMCA A1-004-P-0054	8.4	10.5	Tihange, Belgium
Oreochromis niloticus	RMCA 94-010-P-0004	8.5	10.5	Esna, Egypt
Oreochromis niloticus	RMCA 94-021-P-0016	9.0	11.0	Esna, Egypt
Oreochromis niloticus	RMCA 94-021-P-0014	9.5	12.0	Esna, Egypt
Oreochromis niloticus	RMCA 94-021-P-0035	10.5	13.0	Esna, Egypt
Oreochromis niloticus	RMCA 93-087-P-0035	12.0	15.0	Luxor, Egypt
Oreochromis niloticus	RMCA 86-016-P-0293	14.5	17.0	Niger
Oreochromis niloticus	RMCA 88-023-P-0271	15.0	18.0	Niger
Oreochromis niloticus	RMCA 93-087-P-0009	15.0	18.5	Luxor, Egypt
Oreochromis niloticus	RMCA 88-023-P-0300	18.0	22.0	Niamey, Niger
Oreochromis niloticus	RMCA 88-023-P-0299	18.5	22.0	Niger
Oreochromis niloticus	RMCA 88-023-P-0280	24.5	30.0	Niamey, Niger
Oreochromis niloticus	RMCA 88-023-P-0003	43.0	52.0	Lake Nasser, Egypt
Oreochromis niloticus	RMCA 88-023-P-0111	?	?	Egypt
Sarotherodon galilaeus	RMCA 94-021-P-0050	8.5	10.5	Esna, Egypt
Sarotherodon galilaeus	RMCA 93-158-P-0053	9.0	11.5	Esna, Egypt
Sarotherodon galilaeus	RMCA 94-021-P-0048	9.5	11.0	Esna, Egypt
Sarotherodon galilaeus	RMCA 88-023-P-0027	10.0	12.0	Lake Nasser, Egypt
Sarotherodon galilaeus	RMCA 94-021-P-0046	10.5	12.5	Esna, Egypt
Sarotherodon galilaeus	RMCA 88-023-P-0088	14.0	17.0	Lake Nasser, Egypt
Sarotherodon galilaeus	RMCA 88-023-P-0274	15.0	18.0	Niamey, Niger
Sarotherodon galilaeus	RMCA 88-023-P-0273	16.5	19.5	Niamey, Niger
Sarotherodon galilaeus	RMCA 88-023-P-0018	20.0	25.0	Lake Nasser, Egypt
Sarotherodon galilaeus	RMCA 88-023-P-0297	22.0	27.5	Niger
Sarotherodon galilaeus	RMCA 88-023-P-0087	23.0	29.0	Lake Nasser, Egypt
Sarotherodon galilaeus	RMCA 88-023-P-0021	28.0	35.0	Lake Nasser, Egypt

dal vertebrae. Although we are aware that pharyngeal plates are diagnostic and used in taxonomic studies (*e.g.* Trewavas, 1983), we did not retain these elements as they are very fragile and almost never preserved in an archaeological context. Otoliths have not been considered here either; they are preserved now and then on archaeological sites, but an identification atlas already exists that depicts the otoliths of the taxa dealt with here (Artzi *et al.*, 2009).

While searching for diagnostic criteria enabling the distinction of the three species, special attention was paid to morphological details, as well as to differences in overall shape and proportions of each of the elements. When describing the observed differences, the terminology of Lepiksaar (1994) was used as much as possible. For each bone element, drawings are provided that illustrate the observed differences. For paired elements, it is always the left bone that is illustrated. The diagnostic criteria mentioned in the text are numbered (c.1, c.2, etc.) and indicated on the figures (1, 2, etc.).

In order to evaluate the value of the diagnostic criteria described for the different skeletal elements, two blind tests were carried out on skeletal elements from fish that were not used during the comparative study itself. The outcome also provided information on which taxa are most easily recognized and on the effect fish length has on the described morphological features.

RESULTS

Below the diagnostic criteria of each of the 18 skeletal elements are illustrated and explained in the text.

Premaxilla

The overall shape of the premaxilla can be used for identification (Fig. 1A-F). *S. galilaeus* has a slender processus anterior (p. ant.) and corpus while those of *O. niloticus* are somewhat sturdier. In *C. zillii*, both the processus anterior and processus articularis (p. art.) and the corpus are even sturdier, and the species also stands out by the processus that are short compared to the length of the corpus. In *S. galilaeus,* the base of the processus articularis is not thickened in medial view, while this is the case in the two other species (Fig. 1A-C, criterion 1). The indentation between the processus anterior and the processus articularis is very small in *S. galilaeus*, somewhat larger in *O. niloticus* and is the most pronounced, and clearly deeper, in *C. zillii* (Fig. 1A-C, c. 2). The transition between the processus articularis and the corpus is abrupt in *S. galilaeus* and more gradual in *O. niloticus* and *C. zillii* (Fig. 1A-F, c. 3). The corpus is straight in *S. galilaeus*, in *O. niloticus* it shows a slight downward curve at its posterior end, and the curve is even more pronounced in *C. zillii* (Fig. 1A-F, c. 4). The lateral foramen (lat. for.) between the processus is clearly visible except in *S. galilaeus* where it is rather small and usually unclear (Fig. 1D-F, c. 5). *S. galilaeus* has a narrow margo symphysicus (m. s.) (Fig. 1G-I, c. 6). In *O. niloticus,* it is wider in the lower half, and this broadening can be very pronounced in larger individuals. *Coptodon zillii* has a broad margo symphysicus that is also visible in medial view. The teeth of *S. galilaeus* all have the same size and shape, while the outer row in *O. niloticus* and *C. zillii* has larger teeth (Fig. 1J-L,

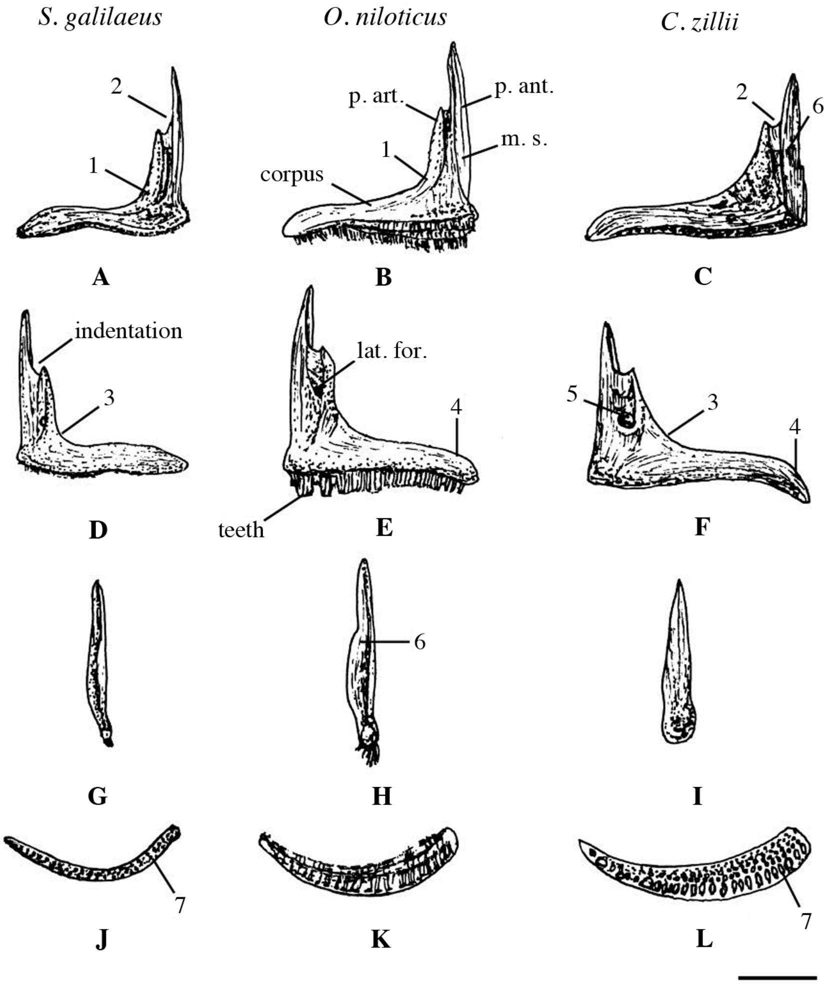

Figure 1. – Premaxilla: medial (**A-C**), lateral (**D-F**), cranial (**G-I**) and ventral (**J-L**) view of the left premaxilla of *S. galilaeus, O. niloticus* and *C. zillii*. Scale bar = 1 cm.

c. 7). Also when the teeth are no longer *in situ*, this criterion is visible through the tooth sockets in the premaxilla. In *O. niloticus,* this criterion is sometimes less clearly visible. In ventral view, the difference in inward curvature of the corpus can be observed (Fig. 1J-L). It is most pronounced in *S. galilaeus* and the least in *C. zillii*.

Dentary bone

The symphysis (s.) of the dentary (Fig. 2) is narrow and low in *S. galilaeus*, broader and higher in *O. niloticus* and the broadest and highest in *C. zillii,* especially in larger individuals (Fig. 2A-I, c. 8). The ventral edge of the symphysis is rounded and never pointed in *S. galilaeus*, it is angular in *O. niloticus* and clearly pointed in *C. zillii* (Fig. 2A-F, c. 9). Besides the five foramina (for.) that are always present on the lateral side of the corpus and processus inferior (p.inf.), there can be one or two additional foramina at the anteriormost part of the processus superior (p. sup.) in both *S. galilaeus* and *O. niloticus (*Fig. 2D-F, c. 10). In *C. zillii,* these foramina occur in a more anterior position, on the corpus itself. Smaller individuals have less visible foramina or there can be even more foramina in these individuals. Individuals of *C. zillii* ranging from 10.5 cm SL to 20 cm SL have a broader processus inferior compared to individuals of the same size of the other two species (Fig. 2A-F, c. 11). The inward curvature of the processus superior is larger in *C. zillii* than in the other two species (Fig. 2G-I). The teeth of *S. galilaeus* all have the same shape and size, while the outer row in *O. niloticus* and *C. zillii* has larger teeth (Fig. 2G-I, c. 12). In *S. galilaeus,* the tooth bearing part consists of the corpus and a small part of the processus superior. In *O. niloticus* and *C. zillii,* a larger part of the processus superior carries teeth (Fig. 2G-I, c. 13).

Maxilla

S. galilaeus and *C. zillii* usually have a rather straight pars caudalis (p. c.) (Fig. 3A-F, c. 14), in *O. niloticus* its dorsal side can be more convex and sometimes shows a bulge. *S. galilaeus* has a crista maxillaris (cr. m.) that, in lateral view, is rather sharp at its anterior side, while it is rounded in the other species (Fig. 3D-F, c. 15). There is a lot of variation in the shape of the processus internus (p. int.) and the processus externus (p. ext.) and also of the tuberositas processus externi (tub. p. ext.). The processus internus is pointed in *S. galilaeus* and it is usually less pointed and rounded in *O. niloticus* and *C. zillii* (Fig. 3A-F, c. 16).

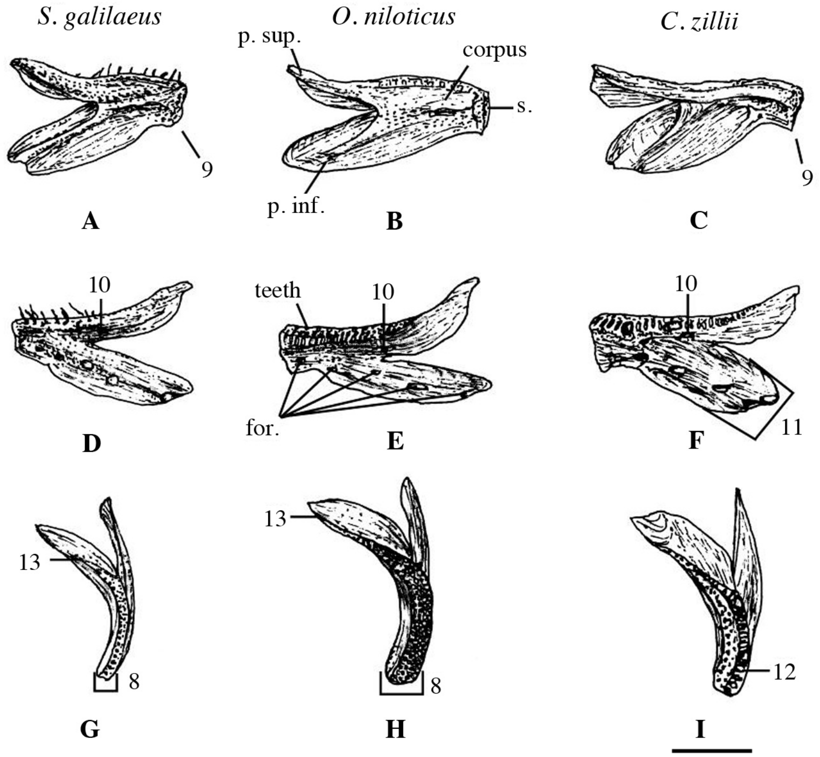

Figure 2. – Dentary: medial (**A-C**), lateral (**D-F**) and dorsal (**G-I**) view of the left dentary of *S. galilaeus, O. niloticus* and *C. zillii*. Scale bar = 1 cm.

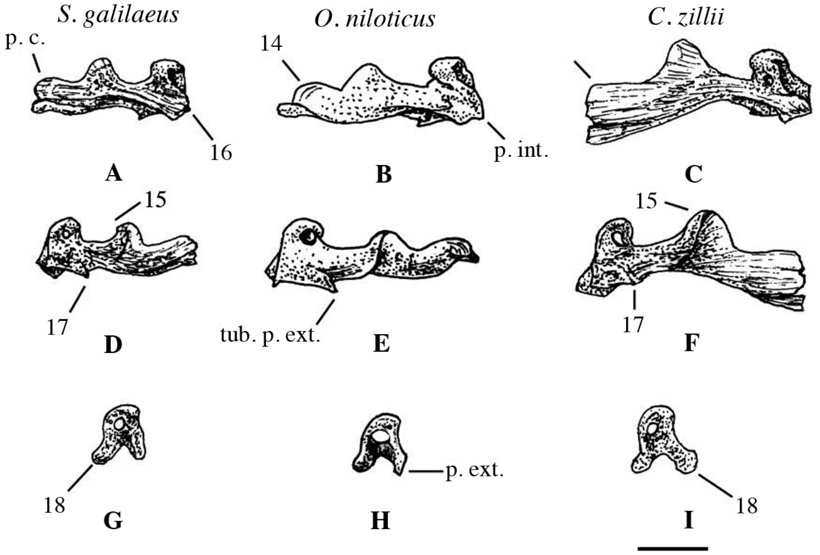

Figure 3. – Maxilla: medial (**A-C**), lateral (**D-F**) and cranial (**G-I**) view of the left maxilla of *S. galilaeus, O. niloticus* and *C. zillii*. Scale bar = 1 cm.

This trend can also be found for the tuberositas processus externi: in *S. galilaeus* it is pointed, in *O. niloticus* it can be pointed or angular, and in *C. zillii* it can be rounded or angular (Fig. 3D-F, c. 17). A better distinguishing character is the proportion between the two processus: the processus internus is longer than the processus externus in *S. galilaeus* and *O. niloticus*. In *C. zillii,* the processus externus is longer and it protrudes more than in the other species (Fig. 3G-I, c. 18).

Articular

The articular bone (Fig. 4) of tilapia has several morphological features that *a priori* seem to make this bone a suitable element for identification. The processus coronoideus (p. cor.) is pointed upwards and the processus anterior (p. ant.) in an anterior direction. The processus ventralis (p. ven.) is pointed downwards and has a channel through it, belonging to the mandibular lateral line canal. At the caudal side the bowl-shaped facies articularis quadrati (f. art. q.) is situated below the processus coronoideus. It appears however that a lot of intraspecific variation occurs, resulting in an overlap of morphology. Only two criteria are retained here which, according to the blind tests, are not always reliable.

The processus anterior (p. ant.) of *S. galilaeus* is slender, while those of *C. zillii* and *O. niloticus* are usually heavier (Fig. 4, c. 19). The processus ventralis (p. ven.) of *C. zillii* does not have a broadening at the end, but stays rather straight. The processus ventralis of *S. galilaeus* and *O. niloticus,* however, do show a broadening at the tip (Fig. 4, c. 20).

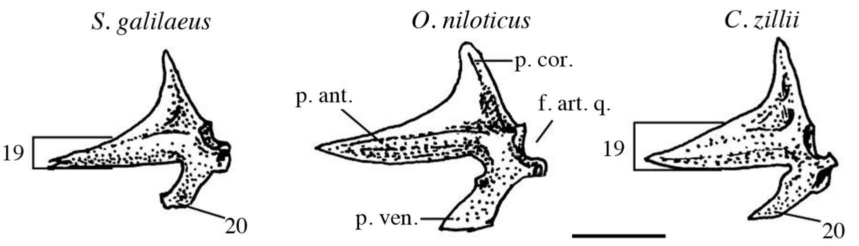

Figure 4. – Articular: lateral view of the left articular of *S. galilaeus, O. niloticus* and *C. zillii*. Scale bar = 1 cm.

Lacrimal

The lacrimal (Fig. 5) of *S. galilaeus* is thicker than that of the other species. Individuals of *O. niloticus* have a clearly shorter lacrimal than those of the other species of the same size (Fig. 5A-F, c. 21). In specimens larger than 20 cm SL, however, the difference becomes less clear. The processus ventralis (p. ven.) is small and blunt or pointed in *S. galilaeus*. *O. niloticus* has a large processus ventralis that can be blunt or pointed, while *C. zillii* has a large and pointed processus ventralis that is clearly separated from the margo ventralis (m. v.) (Fig. 5A-F, c. 22). The costa caudalis (c. c.) of *S. galilaeus* is usually straight and it is concave in *O. niloticus* and *C. zillii* (Fig. 5A-F, c. 23). The processus dorsalis (p. dor.) is small and blunt in *S. galilaeus*, while in *O. niloticus* and *C. zillii* it is large and

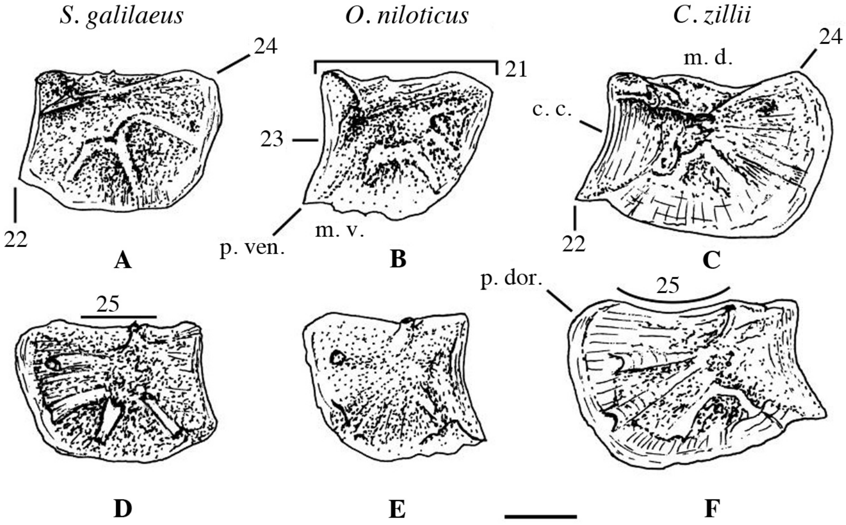

Figure 5. – Lacrimal: medial (**A-C**) and lateral (**D-F**) view of the left lacrimal of *S. galilaeus, O. niloticus* and *C. zillii*. Scale bar = 1 cm.

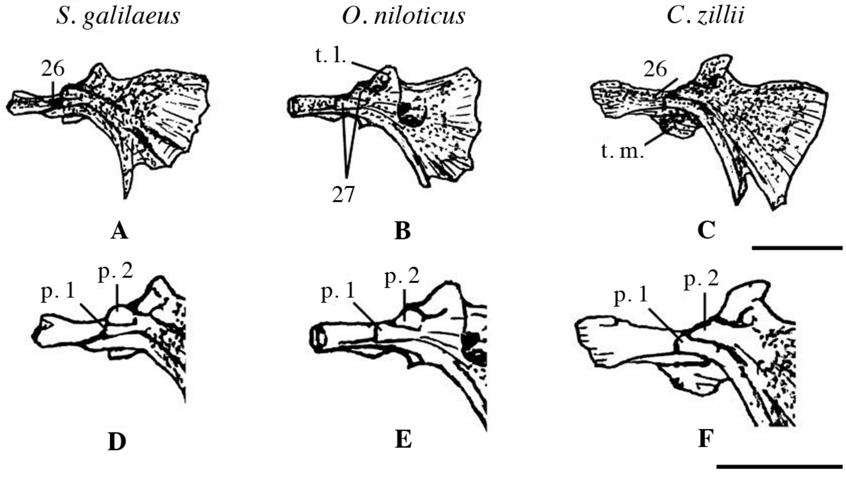

Figure 6. – Palatine: general (**A-C**) and detailed lateral (**D-F**) view of the left palatine of *S. galilaeus, O. niloticus* and *C. zillii*. Scale bar = 1 cm.

rather angular (Fig. 5A-F, c. 24). The lacrimal of *S. galilaeus* has a straight margo dorsalis (m. d.), while in the other two species it is usually curved (Fig. 5A-F, c. 25).

Palatine

In the centre of the palatine (Fig. 6), two tuberculi occur: the lateral tuberculum (t. l.) and the medial tuberculum (t.m.) that cannot be seen easily on these figures. Below the lateral tuberculum, two small processus (p. 1 and p. 2) can be seen. Both the relative position of these processus and their shape allow identification. The two processus of *S. galilaeus* are located above each other, resulting in an upper and a lower processus. Those of *O. niloticus* are placed diagonally with respect to each other. In *C. zillii*, both processus are located behind each other, resulting in an anterior and a posterior processus (Fig. 6A-F, c. 26). Both processus are rounded in *S. galilaeus*, while the first one can also be somewhat more pointed. In *O. niloticus* the first processus is smaller and pointed and the second one larger and rounded. Both processus of *C. zillii* are pointed (Fig. 6A-F, c 27).

Quadrate

The incisura symplecti (i. s.) of the quadrate (Fig. 7) is only a small indentation in *S. galilaeus*, it is clearly incised in *O. niloticus* and forms a deep indentation in *C. zillii* (Fig. 7A-C, c. 28). The angle between the margo anterior (m. ant.) and the processus preopercularis (p. pop.) is small in *C. zillii* compared to those in *S. galilaeus* and *O. niloticus* (Fig. 7A-C, c. 29). The processus preopercularis is longer and extends well beyond the margo superior (m. sup.) in *S. galilaeus* and *O. niloticus*, but not in *C. zillii* (Fig. 7A-C, c. 30). The processus preopercularis is slender in *S. galilaeus* compared to the overall broad appearance in *O. niloticus* and *C. zillii* (Fig. 7D-F, c. 31). The condyli (c.) of *S. galilaeus* are smaller than those of the other two species (Fig. 7A-F, c. 32).

Hyomandibula

The crista anterior (cr. ant.) of the hyomandibula (Fig. 8) is narrow in *S. galilaeus*, broad in *O. niloticus* and even broader in *C. zillii* (Fig. 8A-F, c. 33). The ventral end

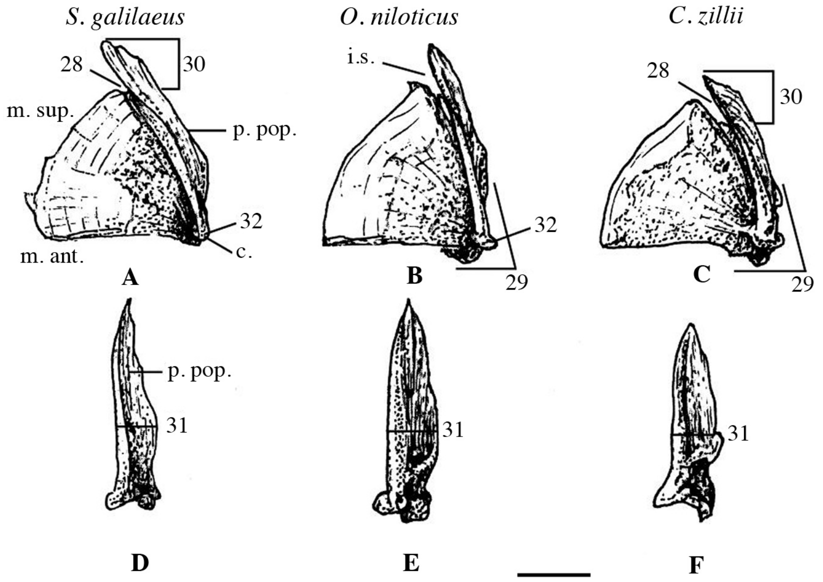

Figure 7. – Quadrate: medial (**A-C**) and caudal (**D-F**) view of the left quadrate of *S. galilaeus*, *O. niloticus* and *C. zillii*. Scale bar = 1 cm.

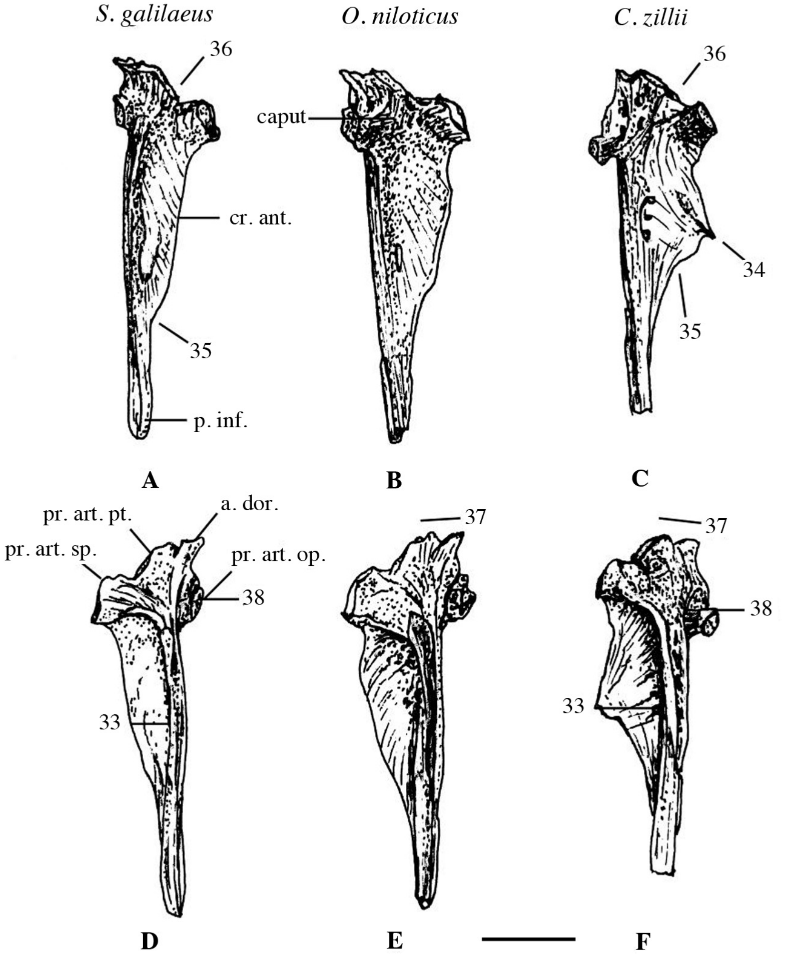

Figure 8. – Hyomandibula: medial (**A-C**) and lateral (**D-F**) view of the left hyomandibula of *S. galilaeus*, *O. niloticus* and *C. zillii*. Scale bar = 1 cm.

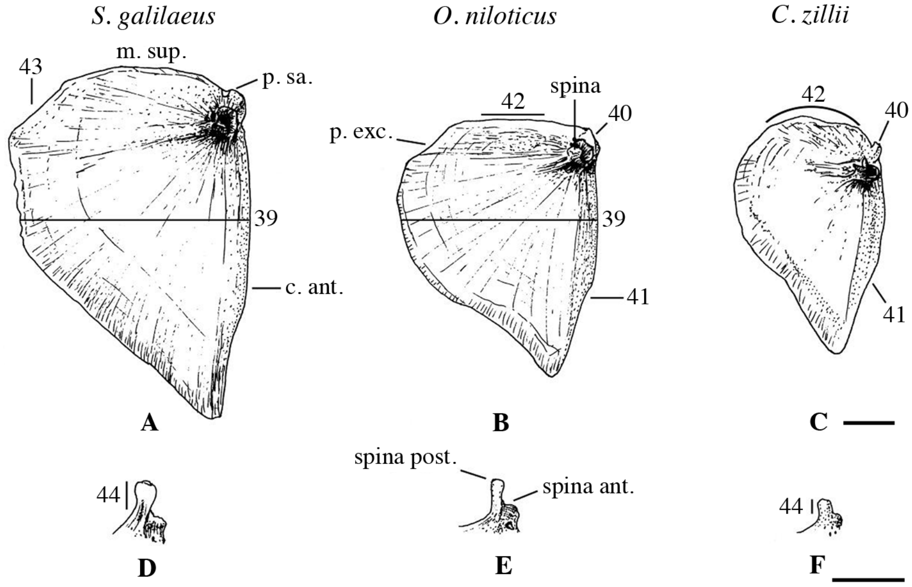

Figure 9. – Operculum: medial view of the left opercle (**A-C**) and detailed view of the spina (**D-F**) of *S. galilaeus, O. niloticus* and *C. zillii*. Scale bar = 1 cm.

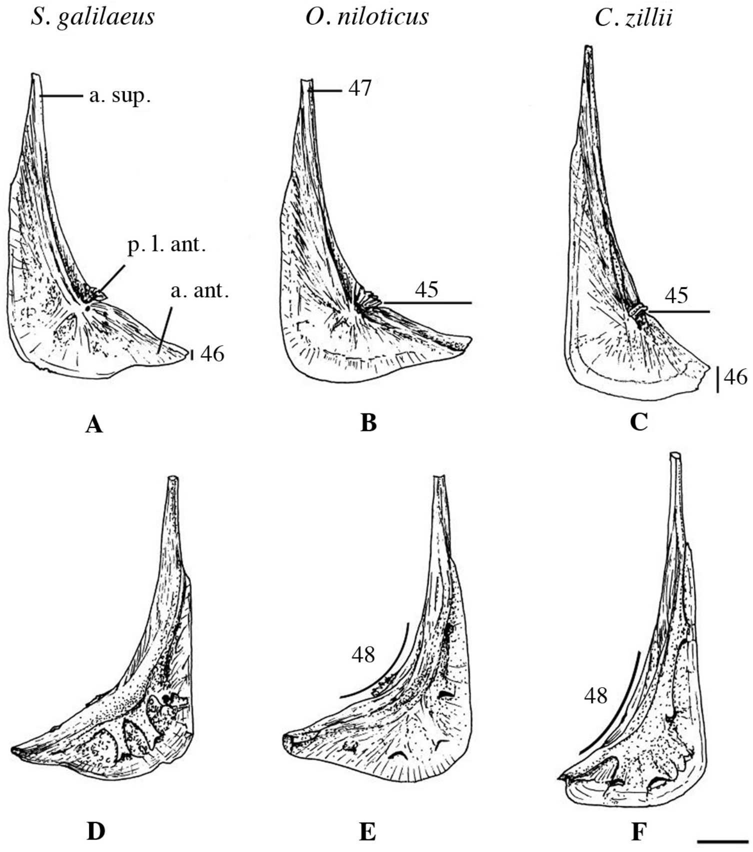

Figure 10. – Preoperculum: medial (**A-C**) and lateral (**D-F**) view of the left preopercle of *S. galilaeus, O. niloticus* and *C. zillii*. Scale bar = 1 cm.

of the crista anterior of *C. zillii* had a clearly pointed spike, while this end is rounded in *S. galilaeus* and *O. niloticus* (Fig. 8A-F, c. 34). *S. galilaeus* and *C. zillii* both show an obvious bend (Fig. 8A-F, c. 35) as a transition between the processus inferior (p. inf.) and crista anterior. This transition is gradual in *O. niloticus*. The aforementioned observations correspond to those described by Murray and Stewart (1999). On the caput of the hyomandibula, three processus can be found: the processus articularis sphenoticus (pr. art. sp.), the processus articularis pteroticus (pr. art. pt.) and the processus articularis opercularis (pr. art. op.). Although the shape of the three processus can show a lot of variation, their relative positions are constant within species. In *S. galilaeus* and *O. niloticus*, there is a smooth transition between the processus articularis sphenoticus and the processus articularis pteroticus, while the two processus are clearly separated from each other in *C. zillii* (Fig. 8A-F, c. 36). The angulus dorsalis (a. dor.) extends well beyond the processus articularis pteroticus in *S. galilaeus* and *O. niloticus* (Fig. 8A-F, c. 37). In *C. zillii,* the angulus dorsalis is lower. The processus articularis opercularis of *C. zillii* is clearly protruding and more separated from the caput compared to the processus of the other two species (Fig. 8A-F, c. 38).

Operculum

The operculum (Fig. 9) is shorter in *S. galilaeus* and *C. zillii* and longer in *O. niloticus* (Fig. 9A-C, c. 39). The processus supra-articularis (p. sa.) shows a lot of variation and can be large and rounded, or pointed in *S. galilaeus* (Fig. 9A-C, c. 40). In *O. niloticus,* this processus can be large but it is most often poorly pronounced, while it is small and rounded in *C. zillii*. A clear bend can be seen about halfway the costa anterior (c. ant.) of *O. niloticus* (Fig. 9A-C, c. 41). In the two other species, this bend is less pronounced and the tapering in a ventral direction is more gradual. The margo superior (m. sup.) is convex in *C. zillii* and *S. galilaeus*, flat or slightly convex in *O. niloticus* (Fig. 9A-C, c. 42). A posterodorsal excavation (p. exc.) is absent in *C. zillii* and is always present in *O. niloticus* as also mentioned by Murray and Stewart (1999), but we noticed this feature also regularly in *S. galilaeus* including in the specimen figured here (Fig. 9A-C, c. 43). The posterior part of the spina is much longer than the anterior part in *S. galilaeus* and *O. niloticus*. In *C. zillii*, it is only slightly longer (Fig. 9D-F, c. 44).

Preoperculum

The shape of the processus s. limbus anterior (p. l. ant.) of the preoperculum (Fig. 10A-F, c. 45) shows a lot of variation in each species and even within one individual the left and right bone can differ in shape. However, the three species can easily be recognized by their angulus anterior (a. ant.) that is long and slender in *S. galilaeus*, long and high in *O. niloticus* and short and high in *C. zillii* (Fig. 10A-F, c. 46). Similar trends can also be found in the angulus superior (a. sup.), but they are less obvious: the angulus is high and slender in *S. galilaeus*, high and broad in *O. niloticus* and lower and broad in *C. zillii* (Fig.10A-F, c. 47). The transition between both anguli is more gradual in *C. zillii* compared to the other two species (Fig. 10A-F, c. 48).

Posttemporal

The length of the processus superior (p. sup.) and the processus inferior (p. inf.) of the posttemporal (Fig. 11) can vary within a species and even between left and right of the same individual. However, in general the processus superior is long in *S. galilaeus* and *O. niloticus*, and relatively short in *C. zillii* (Fig. 11A-F, c. 49). The processus inferior is usually rather slender in *S. galilaeus* and *O. niloticus* and sturdier in *C. zillii* (Fig. 11A-F, c. 50). *O. niloticus* can have an angulus anterior inferior (a. ant. inf.) on the processus inferior (Fig. 11E, c. 51). The canalis lineae lateralis (c. lin. lat.) of *S. galilaeus* is only visible in individuals smaller than 12 cm SL (Fig. 11D-F, c. 52). In *O. niloticus* and *C. zillii,* this channel is usually clearly visible. The anterior pore (po. ant.) of the lateral line canal points in an anterior direction in *S. galilaeus* and in a more dorsal direction in *C. zillii* (Fig. 11D-F, c. 53). In *O. niloticus,* it can be either in an anterior or dorsal direction. We observed a lot of variation in the curvature of the processus superior and in the shape of its anterior end and came to the conclusion that the diagnostic criteria defined by Murray and Stewart (1999) do not hold.

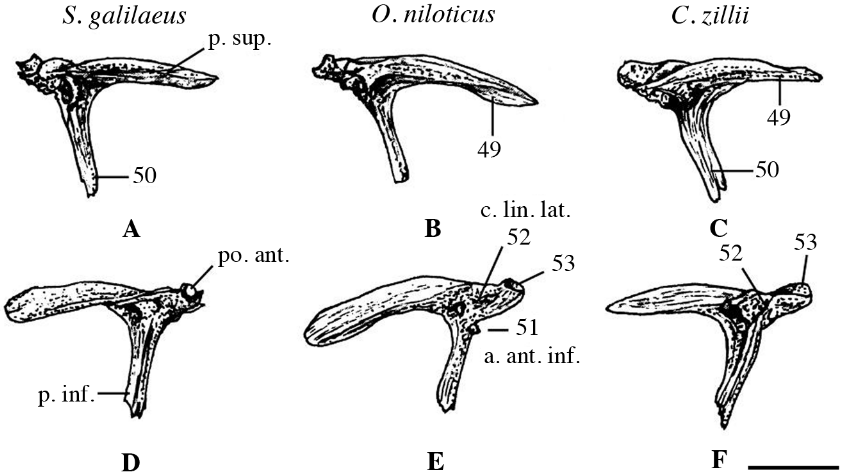

Figure 11. – Posttemporal: medial (**A-C**) and lateral (**D-F**) view of the left posttemporal of *S. galilaeus, O. niloticus* and *C. zillii*. Scale bar = 1 cm.

Cleithrum

The lamina dorsalis (lam. dor.) is slender in *S. galilaeus* while it is clearly broader in *O. niloticus* and *C. zillii* (Fig. 12G-I, c. 54). Also, the lamina externa (lam. ext.) is shorter in *S. galilaeus* than in the other two species (Fig. 12A-F, c. 55). Murray and Stewart (1999) mention an acute notch in the posteroventral edge of the lamina externa in *Oreochromis*, that is said to be less pronounced in *Sarotherodon* and absent in *Coptodon* (Fig. 12D-F, c. 56). This corresponds to our observations, except that an acute notch can also occur in *C. zillii* measuring more than 15 cm SL. The apertura canalis cristae ventralis (apertura) is narrow in *O. niloticus* and broad in *C. zillii*, but it can be either narrow or broad in *S. galilaeus* (Fig. 12A-C, c. 57). *S. galilaeus* and *O. niloticus* have a long spina dorsalis (s. dor.) while it is short in *C. zillii* (Fig. 12A-F, c. 58). The spina dorsalis of *O. niloticus* can also show a bend (Fig. 12B, c. 59). The angulus posterior (a. post.) is large in *O. niloticus* and small in *C. zillii*, but it can be either small or large in *S. galilaeus* (Fig. 12A-F, c. 60). *C. zillii* has a slender and pointed angulus anterior (a. ant.) while *O. niloticus* and *S. galilaeus* have a broad angulus anterior that can vary in shape (Fig. 12A-F, c. 61). The angle between the upper and the anterior part of the cleithrum is large in *S. galilaeus*, small in *O. niloticus* and intermediate in *C. zillii* (Fig. 12A-F, c. 62).

Supracleithrum

In the description of their new tilapia species, Murray and Stewart (1999) mention the thickness and the width of the posterior flange (*i.e.* the pars cleithralis, p. c.) as well as the general shape of the supracleithrum. They depict the three species that we consider here but do not clearly describe the distinguishing characters.

We noticed that the pars cleithralis is clearly higher in *C. zillii* than in the other two species (Fig. 13, c. 63). In *S. galilaeus* and *O. niloticus,* the pars cleithralis only protrudes posteriorly in the central part of the supracleithrum, while it also protrudes in the lower part in *C. zillii*. The pars cleithralis is also broader in *C. zillii* than in the other species. *Oreochromis niloticus* is sometimes somewhat narrower than *S. galilaeus* – when considering specimens of the same length (Fig. 13, c. 64). The costa in *O. niloticus* and *S. galilaeus* is thicker on the lower end, compared to *C. zillii* (Fig. 13, c. 65).

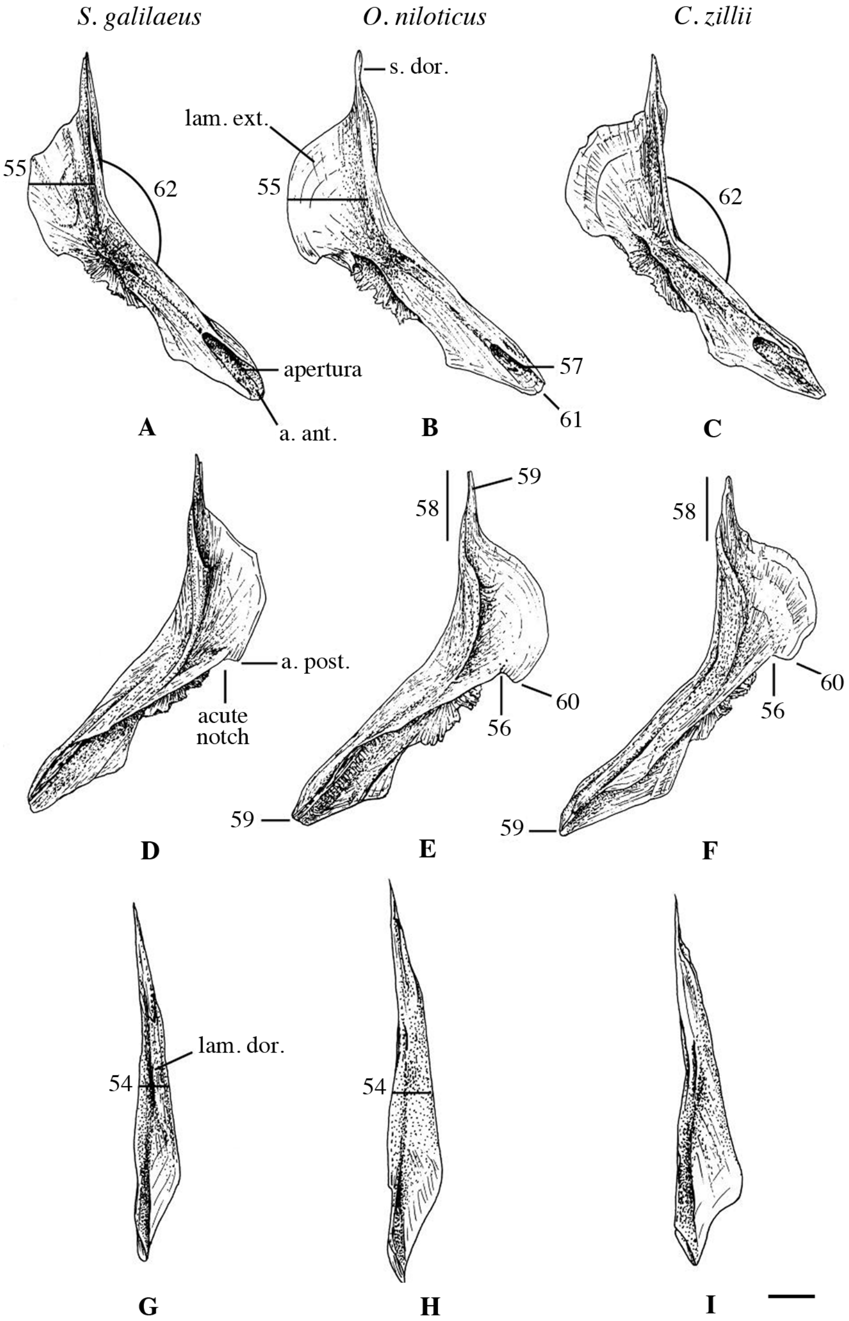

Figure 12. – Cleithrum: medial (**A-C**), lateral (**D-F**) and anterior (**G-I**) view of the left cleithrum of *S. galilaeus, O. niloticus* and *C. zillii*. Scale bar = 1 cm.

Urohyal

There are differences in the proportions of the urohyal (Fig. 14) that allow recognizing the three taxa. The urohyal of *C. zillii* is shorter than that of *S. galilaeus* and *O. niloticus* (Fig. 14A-F, c. 66). Individuals of *S. galilaeus* have a narrow urohyal, compared to those of *O. niloticus* that are broad (Fig. 14A-C, c. 67) and those of *C. zillii* that can sometimes be broad. The urohyal is low in *O. niloticus* and clearly higher in *C. zillii*, but in *S. galilaeus* the urohyal can be either low or high (Fig. 14D-F, c. 68). A lot of variation is observed in the overall shape of the spina (Fig. 14D-F, c. 69). The spina is usually pointing upwards in *S. galilaeus* and *C. zillii* while in *O. niloticus* it is often bent down towards the body of the urohyal. The spina can be blunt or rounded in *S. galilaeus*, it is usually sharp and pointed in *C. zillii* and *O. niloticus*. The collum of *S. galilaeus* is shorter than that of the other species (Fig. 14A-F, c. 70). The condyli differ between the three species. In *S. galilaeus,* both condyli are completely fused together and form a single articular unit, while they are usually clearly separated in *C. zillii* (Fig. 14A-C, G-I, c. 71). The situation is intermediate in *O. niloticus* where the condyli lie closely next to each other, but where they can still be distinguished.

Vomer

In *S. galilaeus* and *O. niloticus,* the vomer is relatively broad, while that of *C. zillii* is narrow (Fig. 15A-F, c. 72). *C. zillii* has a longer vomer, compared to that of the other species albeit that this cannot be clearly seen on the illustrations since the specimen of *C. zillii* used for the illustration is smaller than those of the other species (Fig. 15A-F, c. 73). In dorsal view, the medial edges of the lateral wings diverge abruptly in a caudal direction in *S. galilaeus* and *O. niloticus* whereas they diverge more gradually in *C. zillii* (Fig. 15A-C, c. 74). The lateral wings in *S. galilaeus* and *O. niloticus* broaden more than in *C. zillii* (Fig. 15A-F, c. 75). At the margo anterior, a clear protrusion can only be seen in *O. niloticus* (Fig. 15A-F, c. 76). In *S. galilaeus,* there is rarely a slight protrusion; the margo anterior is usually straight. The margo anterior of *C. zillii* sometimes shows a slight protrusion.

First vertebra

Identification of the first vertebra (Fig. 16) can be done on the basis of its overall appearance in cranial view. In *S. galilaeus,* the corpus and the apohyses (apo.) of the first vertebra form a narrow structure, whereas – when consid-

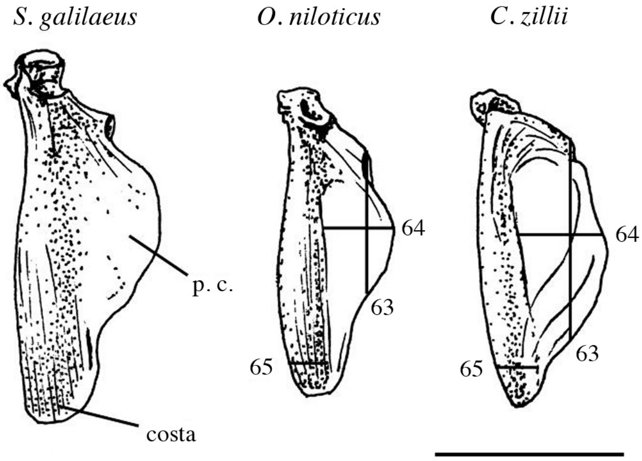

Figure 13. – Supracleithrum: lateral view of the left supracleithrum of *S. galilaeus, O. niloticus* and *C. zillii*. Scale bar = 1 cm.

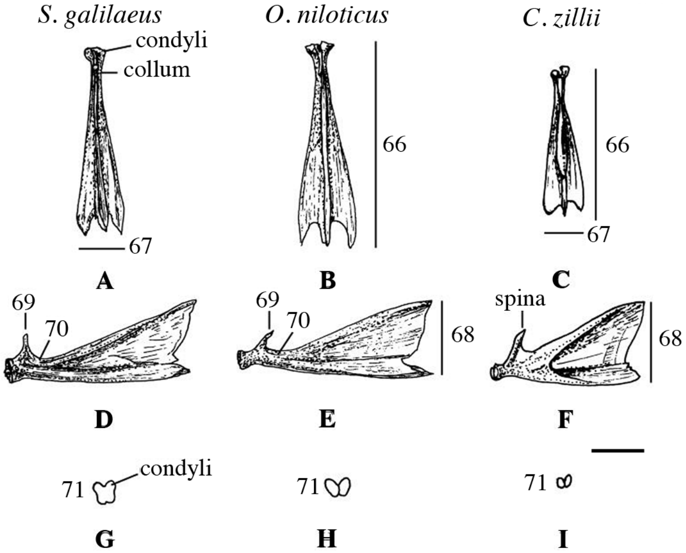

Figure 14. – Urohyal: dorsal (**A-C**), left lateral (**D-F**) and cranial (**G-I**) view of the left urohyal of *S. galilaeus, O. niloticus* and *C. zillii*. Scale bar = 1 cm.

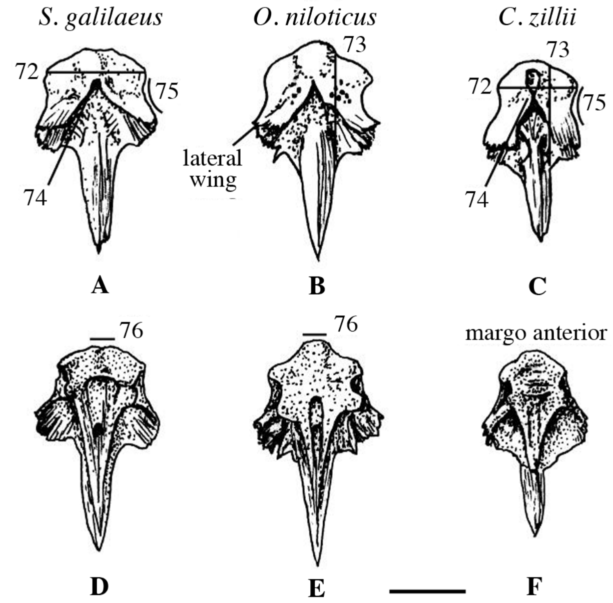

Figure 15. – Vomer: dorsal (**A-C**) and ventral (**D-F**) view of the vomer of *S. galilaeus, O. niloticus* and *C. zillii*. Scale bar = 1 cm.

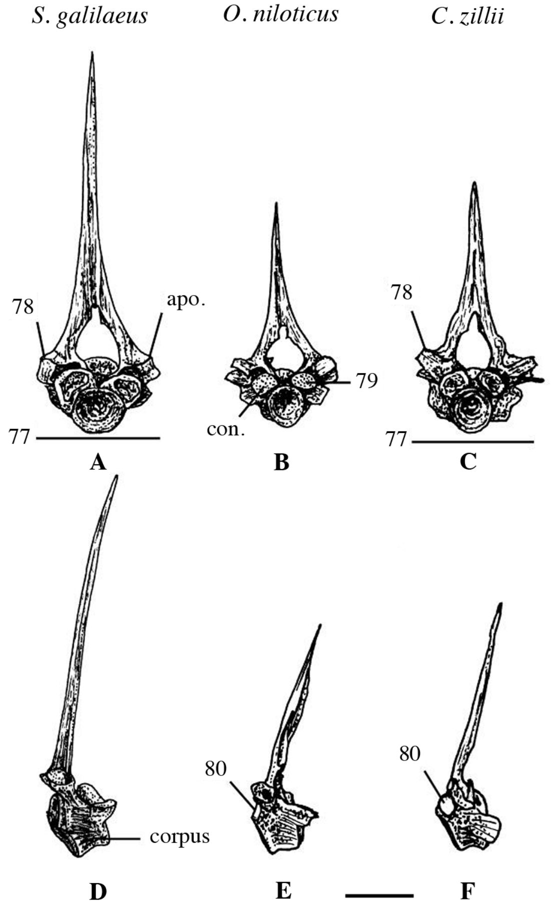

Figure 16. – First vertebra: cranial (**A-C**) and left lateral (**D-F**) view of the first vertebra of *S. galilaeus, O. niloticus* and *C. zillii*. Scale bar = 1 cm.

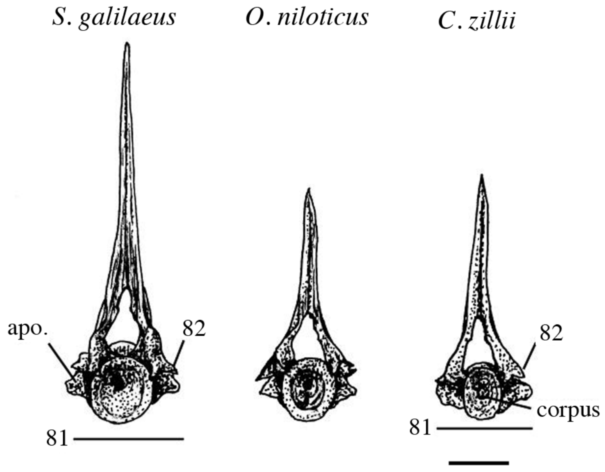

Figure 17. – Second vertebra: cranial view of the second vertebra of *S. galilaeus, O. niloticus* and *C. zillii*. Scale bar = 1 cm.

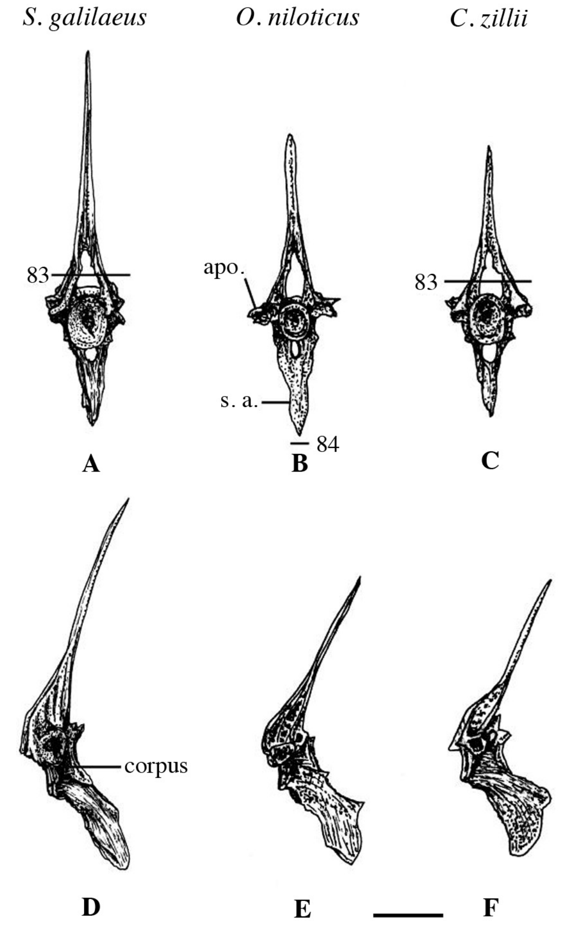

Figure 18. – Third vertebra: cranial (**A-C**) and left lateral (**D-F**) view of the third vertebra of *S. galilaeus, O. niloticus* and *C. zillii*. Scale bar = 1 cm.

ering specimens of the same length – they are broader in *O. niloticus* and the broadest in *C. zillii* (Fig. 16A-C, c. 77). The shape of the apophyses is very variable and identifications should therefore not be based on this sole criterion (Fig. 16A-C, c. 78). They can be narrow, simple and rounded in *S. galilaeus*. In *O. niloticus*, the apophyses are more complex in shape, and they are broader and pointed. In *C. zillii* they are very broad and pointed. The condyli (con.) can have a round, oval or triangular shape in *S. galilaeus* (Fig. 16A-C, c. 79). In *O. niloticus,* they can be round, triangular or kidney shaped. In *C. zillii,* oval, triangular or kidney shaped condyli can be seen. In lateral view, the condyli of *S. galilaeus* and *O. niloticus* are usually not clearly visible but in *C. zillii* they are (fig. 16D-F, c. 80).

Second vertebra

The second vertebra (Fig. 17) can be identified on the basis of the relative width of the corpus and apophyses (apo.). In cranial view, the second vertebra of *S. galilaeus* is narrow, while they are broader in *O. niloticus* and *C. zillii* of the same body length (Fig. 17, c. 81). The apophyses vary in shape. They are smaller in *S. galilaeus*, large and pointed in *O. niloticus*, and large and rounded in *C. zillii* (Fig. 17, c. 82).

Third vertebra

The third vertebra (Fig. 18) shows a lot of variation in the length of the corpus and its overall shape, and in the direction, width and height of the spondylophysial apophysis (s. a.). The third vertebra of *C. zillii* is usually broader compared to that of the other species (Fig. 18A-C, c. 83). The spondylophysial apophysis is usually broader in cranial view in *O. niloticus* (Fig. 18A-C, c. 84). This is however not always the case. Because of the large variation and the limited number of criteria, the third vertebra is of limited use for identification.

DISCUSSION AND CONCLUSIONS

The blind tests (Tab. II) largely reflect the findings described above and show that most of the 18 elements studied here are suitable for identification. During each of the two blind tests, 10 specimens were selected (by WW) for each of the skeletal elements. The corresponding fish lengths ranged between 7.0 and 18.5 cm SL, with most of the individuals measuring between 9 and 11 cm SL. During the identification (by KD), the drawings and the description of the morphological criteria were used, but this was always done in combination with a consultation of actual modern specimens. Bones of fish measuring less than 7 cm SL were not used in the blind tests as a quick preliminary analysis of the skeletons of such small animals had shown that the distinguishing characters are not yet clearly developed in juveniles.

Table II. – Correct identifications during the two blind tests.

Element	Blind test 1	Blind test 2	Success rate
Premaxilla	8/10	7/10	75%
Dentary	10/10	10/10	100%
Maxilla	8/10	9/10	85%
Articular	6/10	4/10	50%
Lacrimal	10/10	10/10	100%
Palatine	8/10	9/10	85%
Quadrate	10/10	9/10	95%
Hyomandibula	10/10	9/10	95%
Operculum	10/10	10/10	100%
Preoperculum	10/10	10/10	100%
Posttemporal	7/10	7/10	70%
Cleithrum	7/10	9/10	80%
Supracleithrum	7/10	7/10	70%
Urohyal	7/10	9/10	80%
Vomer	8/10	6/10	70%
First vertebra	9/10	10/10	95%
Second vertebra	7/10	7/10	70%
Third vertebra	4/10	2/10	30%

Based on the scores of the blind tests, we recommend to not use the third vertebra and the articular for identification. The third vertebra is a rather simple skeletal element with only a limited number of morphological features that, in addition, show a lot of variation. The poor results obtained in the identification of the articulars confirm what has already been mentioned in the description above, namely that this element, despite its numerous morphological features, does not display reliable criteria.

The other skeletal elements give good to very good results with a 100% correct identification for the dentary, lacrimal, operculum and preoperculum and 95% correct attribution in the case of the quadrate, the hyomandibula and the first vertebra. It appears that most often misclassifications are due to the fact that the skeletal elements are derived from rather small individuals in which the morphological features are not yet clearly developed. The fact that somewhat less correct identifications were obtained during the second blind test is related to the smaller average size of the fish selected for this test.

From the description of the diagnostic characters it appears that in many cases *Coptodon* stands out clearly from the other two genera: this is the case for the premaxilla, dentary, maxilla, lacrimal, palatine, quadrate, hyomandibula, operculum, preoperculum, urohyal and vomer. Also during the blind tests it was noticed that *Sarotherodon* and *Oreochromis* resemble each other more which resulted sometimes in wrong identifications. The differences between *Coptodon* and on the other hand *Sarotherodon* and *Oreochromis* can most likely be linked to their reproductive behaviour. Peters (1961) and Goedel (1974) already stated that substrate spawning tilapias (*Coptodon*) have a more slender, higher and shorter head than mouth brooding tilapias (*Sarotherodon* and *Oreochromis*).

In conclusion, it can be said that a distinction of the tilapiine genera *Coptodon*, *Sarotherodon* and *Oreochromis* is possible on most of the skeletal elements analysed. We recommend to not only use the descriptions and drawings provided in this paper for the identification of isolated bone elements, but to include also three-dimensional comparisons of the fossil bone with modern specimens, preferentially of different sizes. For each skeletal element several diagnostic criteria are provided and it is recommended to consider them simultaneously to ameliorate the identifications. The morphological characteristics described here will allow more accurate identification of fossil and subfossil finds of tilapia and thus enable better documenting the zoogeographical history of these taxa. Examples where the present study can be expected to provide more results are for instance the expansion and retraction of tilapia populations in the Sahara as a result of changing climatic conditions during the Quaternary (Van Neer, 1989) or on a broader Cenozoic timescale for the entire Nile basin (Stewart, 2009).

Acknowledgements. – The drawings of the skeletal elements were made by Anne-Marie Wittek (ADIA, Association pour la Diffusion de l'Information Archéologique). This paper presents research results of the Interuniversity Attraction Poles Programme – Belgian Science Policy.

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